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EVOLUTION OF LIFE HISTORIES: A COMPARISON OF *ANOLIS* LIZARDS FROM MATCHED ISLAND AND MAINLAND HABITATS

Robin M. Andrews[1]

Abstract. Faunal comparisons between islands in the West Indies and the South and Central American mainland suggest that *Anolis* lizards play very different trophic roles in these two regions. Island anoles, with few predators, appear to be food limited relative to the heavily preyed upon mainland species. Theoretical considerations of species living under different competitive regimes suggest that island and mainland anoles should have evolved major differences in their life histories.

In order to evaluate the evolution of life history in the genus *Anolis*, I consider the degree of food limitation for anoles in comparable island and mainland habitats, the life history consequences of different selective regimes, and the correlation between observed life histories and theoretical expectations. Food availability on island and mainland sites was assessed from determinations of the standing crop of arthropods relative to the standing crop of anoles. A more direct assessment was accomplished by evaluating growth rates of *Anolis* juveniles. Both comparisons indicate that island anoles are food limited relative to mainland counterparts. Island anoles exhibit delayed maturity, long adult survivorship, large adult size, high sexual dimorphism ratios, and probably low reproductive effort in comparison with mainland anoles of similar size. For the most part, observed life histories fit the predictions based on current life history theory. However, for a given population, maximum body size, sexual dimorphism ratios, and offspring size are relatively invariant in expression. On the other hand, growth rate, rate of egg production, and age at sexual maturity vary as a function of food availability.

INTRODUCTION

In this paper I evaluate the effects of the competitive milieu on evolution of life history in the lizard genus *Anolis*. Various observations suggest the island and mainland members of this large group differ in the way that their populations are regulated. Anoles of the South and Central American mainland have numerous competitors for their insect prey and also have many predators; these anoles play minor roles in the middle levels of their complex food webs (Rand and Humphrey, 1968). On the other hand, anoles of the West Indies have few competitors or predators. There are fewer species of birds on these islands than in comparable mainland habitats and many types of insectivorous and lizard-eating birds are totally absent. These missing species include motmots, antbirds, woodhewers, ovenbirds, and puffbirds (Bond, 1971). Moreover, West Indian bird faunas do not exhibit density increases as a result of fewer species; density of insectivorous birds is lower in the West Indies than in comparable mainland habitats (Recher, 1970; Terborgh, pers. comm.). At a given West Indian site there tend to be fewer species of frogs (possible competitors for small insect prey) and snakes (possible predators on lizards) than at a comparable mainland site. The number of lizard species is also often lower than on the mainland (Rand, 1961; Schwartz and Thomas, 1975). Army ants which compete with anoles on the mainland have never reached the West Indies. It is this poverty of potential competitors that allows Williams (1972) to conclude that competition among West Indian anoles is, for all practical purposes, intrageneric.

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[1] Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

Trophic level differences suggest that island anoles, with few predators, may be food limited relative to the heavily preyed upon mainland species (Slobodkin et al. 1967; Wiegert and Owen, 1971). Recent theory predicts that such differences in mode of population regulation might have profound effects on *Anolis* life histories (MacArthur and Wilson, 1967; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Pianka, 1970, 1972).

The effect of the competitive milieu on the allocation and utilization of energy result in the predictions listed in Table 1. Heightened competition in saturated environments will either 1) reduce the overall amount of energy that an organism can gather per unit time or 2) force changes in the allocation of time and energy devoted to conflicting demands, or both will occur (Pianka, 1972). The consequences of this are important. The absolute amount of energy that can be used for reproduction is reduced. Thus a relatively low reproductive effort is predicted for populations in saturated environments. Moreover, selection will usually favor

Table 1. Predictions of relative differences in life history between island and mainland *Anolis* lizards.

	ISLAND ANOLES: Food Limited	MAINLAND ANOLES: Not Food Limited
1. Reproductive effort	Low	High
2. Sexual maturity	Late	Early
3. Relative size of offspring	Large	Small
4. Size	Large	Small
5. Sexual dimorphism in size	High	Low

individuals with attributes that make them successful in competitive situations. In *Anolis*, selection for large size can be expected to be particularly efficacious because larger individuals are usually dominant over smaller individuals in competition for space, which provides an advantage for obtaining food and mates (Rand, 1967; Trivers, 1976). Sexual dimorphism in size is a means by which competition for food between male and female *Anolis* is reduced (Schoener, 1967). High sexual dimorphism ratios are expected when competition is intense. Since juveniles fare poorly in competition with established adults, selection should favor long adult life with reproduction occurring in more than one breeding season (Murphy, 1968). Tinkle et al. (1970) predict that lizards living in saturated environments will have relatively large eggs and hatchlings because of the relationship between size and competitive ability. In sum, island anoles should be K-selected in the sense of MacArthur and Wilson (1967).

On the other hand, if mainland anoles are generally limited by their predators, they should be r-selected relative to island anoles that are limited by food resources (Pianka, 1970, 1972). Because the risk of death is high for all age classes of mainland anoles, fitness is maximized by high reproductive effort. Attributes that maximize present reproduction will be favored by selection because the chance of future reproduction is small. Because age at first reproduction and size are closely and positively related (Fenchel, 1974), selection for early reproduction (which is the most effective way to increase r) will parallel selection for small adult body size.

In order to evaluate the evolution of life history in the genus *Anolis*, I have considered three main questions: Are island anoles food limited relative to mainland anoles? If so, what have been the life history consequences of the different selective regimes? Do the observed life histories conform to theoretical expectations?

To evaluate the hypothesis that island anoles are food limited relative to mainland anoles, I first compare the standing crop biomass of *Anolis* predators and their arthropod prey in comparable island and mainland habitats. A lower ratio of prey to predator biomass on islands than on the mainland would provide indirect evidence supporting the hypothesis. More direct evidence is sought in comparisons which involve the relative allocation of energy to feeding and social interactions as opposed to growth and reproductive effort. The hypothesis will also be tested with data on population turnover. Higher individual persistence in island versus mainland populations would provide evidence that predation pressure is lower in island than in mainland habitats. Next, various life history attributes of island and mainland anoles are contrasted to determine if island and mainland anoles differ in body size, age at sexual maturity, sexual dimorphism ratios, reproductive effort, and size of offspring. Finally, I discuss the evolution of life histories in *Anolis*.

MATERIALS AND METHODS

Comparisons of island and mainland *Anolis* are based on data that I collected from cacao plantations on Dominica (an island) during August 1971, March 1972, and July 1972 and in Costa Rica (mainland) during April and May 1971, August 1971, and February 1972. Cacao plantations were chosen because different localities have similar climates; cacao requires rainforest climates with high, evenly distributed rainfall. In such environments seasonal differences in lizard reproduction are minimal (Licht and Gorman, 1970; Sexton et al., 1971) facilitating comparisons of different sites. Moreover, the closed canopy of a mature cacao plantation and the shade required by the trees themselves make the understory of a cacao plantation similar to that of an undisturbed rainforest (Leston, 1970).

Sites and anoles studied

The island site was located on the windward side of Dominica at Londonderry Estate 2 km N of the Melville Hall Airport at an elevation of about 15 m. Weather stations in this area frequently average over 2500 mm of rain a year and even during the relatively dry period, mid-January to mid-March, rainfall is usually more than 100 mm a month (Beard, 1949; Hodge, 1954). Rainfall at Melville Hall Estate for August 1971 was 268 mm, for March 1972 was 265 mm, and for July 1972 was 108 mm (Christopher Maximae, pers. comm.).

Dominica has a single species of anole, *Anolis oculatus*. On the basis of geographical variation in size and color pattern four subspecies have been described (Lazell, 1972). *A. oculatus winstoni* is found in lowland habitats on the windward side of the island. Subsequent references to *A. oculatus* will apply to this subspecies. *Anolis oculatus* are common in such diverse habitats as beach strand and undisturbed forest but appear to be most abundant in man-made "forests" such as cacao and orange groves. In cacao plantations *A. oculatus* occupy all structural components of the habitat, i.e. individuals are seen on the ground, on trunks, and in the canopy.

The mainland study site was located in the Atlantic lowlands of Costa Rica about 45 km W of Limon (Limon Prov.) on Finca La Lola, the cacao experimental station of the Instituto Interamericano de Ciencias Agricolas (IICA, Turrilaba) at an elevation of 33 m. Average annual rainfall at La Lola for the years 1949-1967 was 3501 mm (Soria et al., 1969). There are two relatively dry periods a year (February-March and September), but rainfall rarely falls below 100 mm a month. Rainfall at La Lola for April 1971 was 266 mm, for May 1971 was 111 mm, for August 1971 was 106 mm, and for February 1972 was 332 mm (Alfredo Paredes, pers. comm.).

Although seven species of anoles are recorded from nearby forests, only two are commonly found in the cacao plantations (Talbot, 1977). Of these, *A. limifrons* is by far the most abundant, being found in all localities where shade is present. In the cacao, individuals are usually found less than 2 m above the ground but seldom on the ground itself. In contrast, the terrestrial *A. humilis* is restricted to older cacao stands where understory vegetation is sparse.

Mark-recapture studies

Mark-recapture studies, conducted during three visits over about a year, were made in mature cacao plantations characterized by a continuous canopy and sparse understory. In Dominica, the 625 m^2

study site included 43 regularly spaced cacao trees and six large breadfruit trees (Fig. 1). In Costa Rica, the 652 m² study site (in Experimental Section 19 of Finca La Lola) included 45 regularly spaced cacao trees and two large *Hura crepitans* (Fig. 2). Insecticides or other chemical treatments were not used on the study sites during this study or for many years previously.

During census periods, anoles were captured by hand and information on size, sex, individual identification number, and location were recorded in the field. Anoles were released shortly after capture where they were caught. Snout-vent length (SVL) was measured to the nearest mm for each capture and during some census periods weight (W) was determined to the nearest one-tenth of a gram (Pesola scales). Sex of adults and all but the smallest juveniles was readily distinguishable by the presence of the large dewlap in males only. Additionally, male *A. oculatus* of all sizes have enlarged post-anal scales which females lack. Individuals were identified by clipping the terminal phalange of toes in unique combinations involving not more than one toe.

Population size was estimated from mark-recapture data. For *A. oculatus,* I estimated population size with the Peterson method using a normal approximation to place 95% confidence intervals around the mean (Seber, 1973). Census data for these estimates were collected on 17–20 March and 30 March-1 April, 1972. For *A. limifrons,* population size was estimated with a regression procedure (Marten, 1970) using data of five census periods during April and May 1971.

Adult survivorship on the study sites was determined from the proportion of marked adults collected during the two site visits after the initial marking period.

Diet analyses

Anoles were collected[2] for stomach-content analysis in cacao plantations adjacent to and similar in vegetation structure to the mark-recapture sites. On Dominica, this collection was made on two days in August 1971, and in Costa Rica, on six days in early May 1971. Collections were made in late afternoon on rainless days so that all individuals had an equal time to feed. Individuals were

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[2] These collections have been deposited in the Museum of Comparative Zoology, Harvard University.

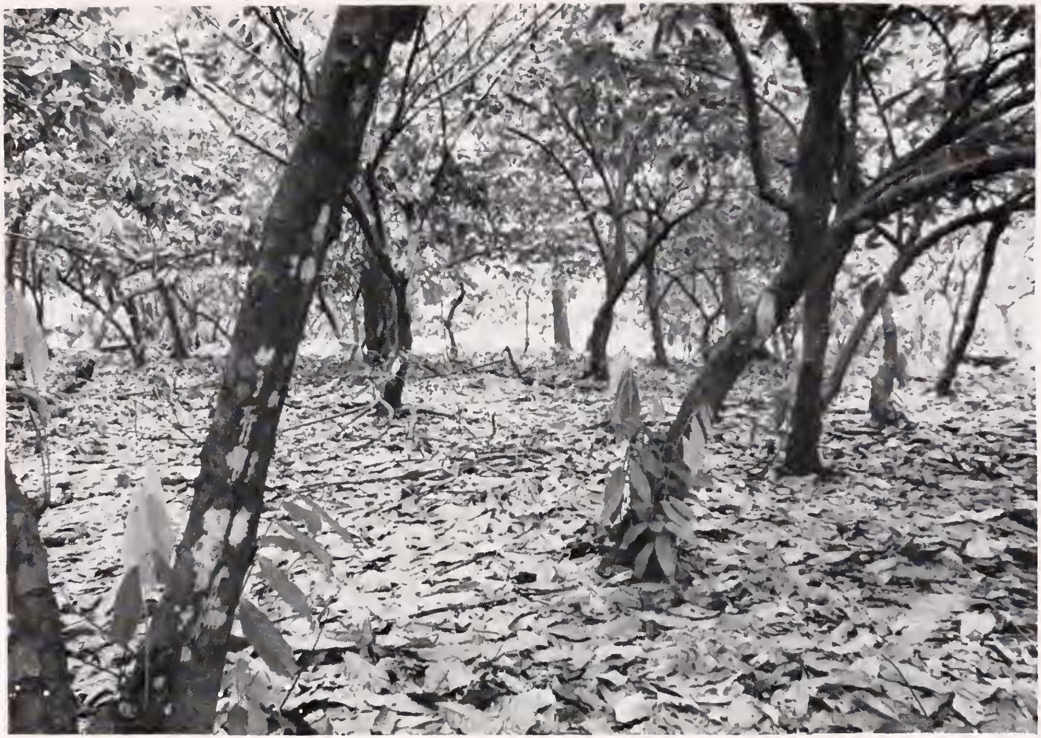

Fig. 1. Study site in cacao plantation in Dominica, W.I.

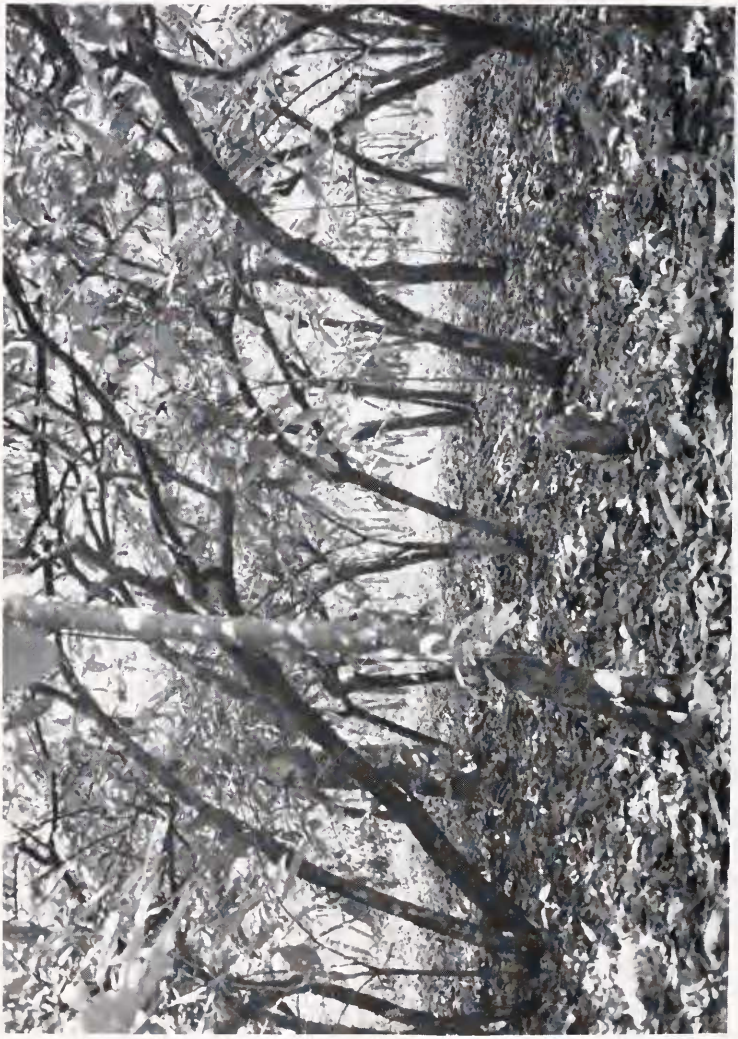

Fig. 2. Study site in cacao plantation in Costa Rica.

collected by size in proportion to their occurrence in the populations. Specimens were killed within an hour of capture and preserved in alcohol.

Stomach contents were analyzed using the following techniques. The length of each item found in the stomach proper was measured and the average width and depth were estimated to the nearest 0.1 mm with an ocular micrometer. The volume of each arthropod was determined by multiplying these three dimensions. Arthropods were assigned to one of 15 taxonomic categories (Table 2).

Anolis *body size and reproductive condition*

For each lizard in the above collections SVL and head length (HL) were measured. Head length was measured as the distance

Table 2. Composition of arthropod collections made by sweeping understory vegetation on the Dominica and Costa Rica cacao sites. Values are percentages of total numbers in each collection and do not include collembola and mites.

	DOMINICA		COSTA RICA	
	cacao foliage	forest foliage	cacao foliage	forest foliage
Lepidoptera larvae	0.2	0.0	1.9	0.3
Lepidoptera adults	0.3	2.7	5.8	0.7
Orthoptera	1.9	0.5	2.3	4.1
Blattidae	0.1	0.0	0.0	1.1
Hymenoptera: Formicidae	40.8	52.5	10.3	21.4
Hymenoptera: Other	10.7	3.1	18.5	12.1
Homoptera	5.5	5.8	10.6	6.4
Hemiptera	1.5	0.0	1.8	0.7
Coleoptera adults	1.2	2.3	13.3	11.2
Diptera adults	32.3	20.6	29.3	21.7
Holometabolous larvae (except Lepidoptera)	0.1	0.0	0.1	0.1
Araneida	4.5	11.8	5.5	6.3
Isopoda	0.0	0.0	0.1	2.4
Isoptera	0.3	0.0	0.0	9.6
Miscellaneous	0.5	0.7	0.5	1.9
Sweeps	700	450	250	350
Total arthropods	3522	3180	1952	1219
No. ⩾ 5 mm/1000 sweeps	243	44	972	526

from the anterior edge of the ear opening to the tip of the snout. The sex of each specimen was confirmed by dissection and the reproductive condition of females was indexed by the number of oviducal eggs and the diameter of the largest ovarian follicle.

The relation of head length and weight to SVL was determined by a least squares analysis. A single regression equation was appropriate for each of the three species because separate analyses for males and females did not alter the equation significantly ($p > 0.05$).

Lizards were classified as adult male, subadult male, adult female, and juvenile. Females were considered adult (sexually mature) at SVLs not less than that of the smallest female with oviducal eggs. For species in which males are considerably larger than females, subadult males are equal in range of SVL to adult females (after Schoener, 1968). Subadult males are small, sexually mature males (Licht and Gorman, 1970; Sexton et al., 1971) that appear to be excluded from the breeding population by the larger adult males (Rand, 1967; Andrews, 1971a) and thus form a separate class. Juveniles, defined as immature individuals, were sometimes divided into two groups: juvenile I and juvenile II, with smaller and larger individuals, respectively.

The total live weight of anoles on each of the study areas was estimated using the following technique. I divided the *A. limifrons* collected in May 1971 and the *A. oculatus* captured in March 1972 into SVL categories separated by 1 mm increments. The appropriate regression equation was used to convert SVL to weight. Weight was then multiplied by the number of individuals in each SVL category and the results were summed within classes to give the total weight per class. These values were adjusted for the estimated number of individuals per class on the study areas.

Behavioral studies

Information on foraging behavior was collected through a series of standard 30-minute observation periods (e.g. focal-animal sampling, Altmann, 1975). Foraging behavior was typified by adult females because foraging is more clearly defined in females than in (adult) males (Andrews, 1971a). On Dominica, observations were made between 6 and 18 August 1971 on the capture-recapture area. On the Costa Rica site, observations were made between 29 April and 10 May 1971 on both the capture-recapture area and the collection area.

Characteristics of arthropod communities

Arthropod abundance, size distribution and taxonomic composition on the cacao study sites and also in undisturbed forests nearby were determined from sweep samples of understory foliage. Sweep samples provide representative collections of the kinds of prey eaten by anoles that forage in this stratum (Andrews, 1971b). The limitations and assets of sweep sampling as an ecological technique are discussed in previous literature (Southwood, 1966; Janzen and Schoener, 1968; Janzen, 1973a).

On the cacao sites, sweep collections for arthropods were made within two days of the collections of anoles and were taken on the same areas as the anole collections. The forest site on Dominica (Palmist Ridge) was located 5 km SW of the cacao site at an elevation of about 275 m. Rainfall is approximately 4000 mm/y. This ridge top forest is extensive, with a high (max. 44 m) and fairly open canopy. The understory is sparse enough to walk through easily at most points. This site is further described by Soriano-Ressy et al. (1970). Sweep samples were taken in this forest in March 1972. The forest site in Costa Rica was located 2 km from Finca La Lola near the road between Limon and Siquirres and at a similar elevation to the cacao site. The forest area was relatively small (perhaps less than 1 km^2) and was surrounded by cacao and areas recently clear cut. Trees had been selectively removed from the forest and therefore in some places the understory vegetation was dense enough to prohibit easy access. Sweep samples were taken in this forest on 29 February 1972.

Methods used for sweep sampling are described by Janzen (1973a). The total number of sweeps on each site ranged from 250 to 700 with sets of 50 separated for statistical purposes. Arthropods were manually sorted from the leaves and detritus immediately after collection and then preserved in alcohol. Sampling was conducted only during sunny or intermittently cloudy conditions and at the same time of day (1000–1200 hours) on both sites. The same methods of taxonomic categorization and measurement of length were used for these arthropods as for the arthropods taken from the *Anolis* stomachs. However, dry weight in each length class was estimated using regression equations (Sage, 1974, Appendix Table 2) rather than from a volumetric determination. The following relationship for adult insects was used for most length classes:

$$\ln Y = -7.761 + 0.3498X - 0.003931X^2$$

where Y = dry weight in grams and X = length in mm. For Lepidoptera larvae and Orthoptera of 15 mm and greater, I used equations specific for these taxa.

RESULTS AND DISCUSSION

Prey Availability: Size, Abundance, and Taxa

Size-frequency distributions of arthropods collected in cacao plantations show that large individuals were poorly represented in the island sample (Fig. 3). Only 4.8% of all individuals were 5 mm or greater in length on the Dominica site in contrast with 12.8% on the Costa Rica site ($p \leqslant .001$, Kolmogorov-Smirnov two-tailed test). This contrast between sites is accentuated when dry weight in each arthropod length class is plotted (Fig. 4) and further illustrated by summing total dry weights per 1000 sweeps, 6.4 g for Dominica and 17.8 g for Costa Rica. Moreover, significantly fewer arthropods were collected on the Dominica site than on the Costa Rica site (Table 2, $p = 0.02$, Mann-Whitney two-tailed test). The Dominica site averaged 247 arthropods per 50 sweeps and the Costa Rica site, 391 arthropods per 50 sweeps. Thus the low abundance of arthropods on the Dominica site is related to, in part, the low numbers of large individuals.

The collection of arthropods from forest understories on Dominica had significantly fewer large arthropods than did the collection from the Costa Rica site (Table 2, $p \leqslant .001$, Kolmogorov-Smirnov two-tailed test). The island site also had a lower dry weight biomass of arthropods per 1000 sweeps than did the mainland site, 6.5 g as opposed to 8.1 g, respectively. However, the Dominica forest collection had significantly more individuals per 50 sweeps than did the Costa Rica forest collection ($p = .02$, Mann-Whitney U test, two-tailed). This is the result of large numbers of one very small myrmicine ant in the Dominica collection.

The taxonomic composition of the arthropod collections on the two sites is contrasted in Table 2. Formicidae dominate the island collections (41–53%) with the one myrmicine species contributing respectively 27.4 and 46.7% of all arthropods collected from the

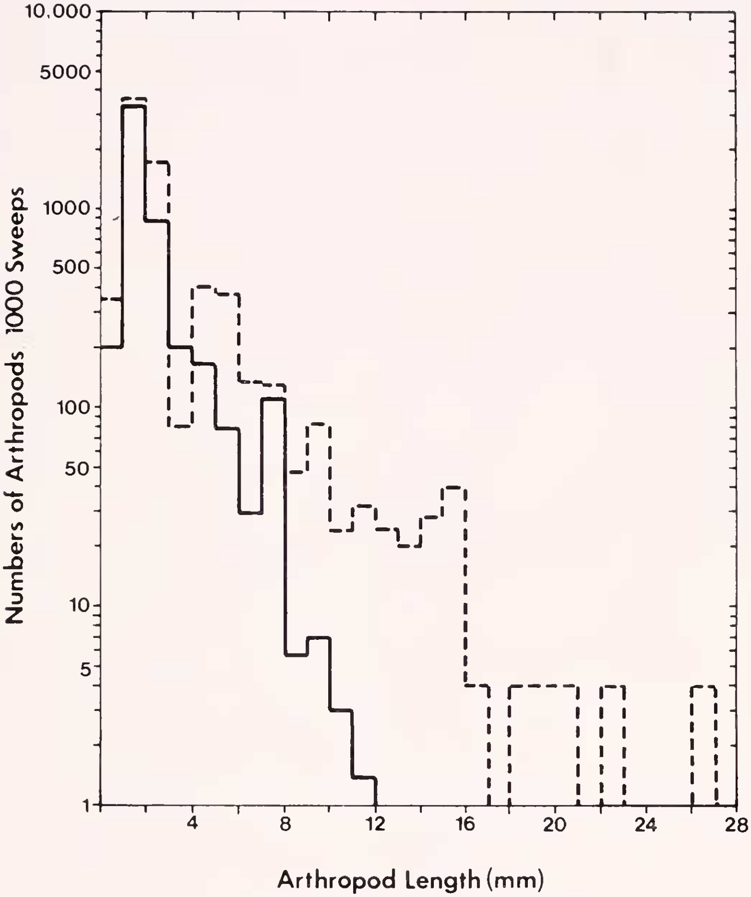

Fig. 3. Size-frequency distributions for arthropods collected in understory foliage in cacao plantations in Dominica (—) and La Lola, Costa Rica (----). Arthropods of 28 mm or more in length are not shown (2 in Dominica and 1 in Costa Rica).

cacao and forest foliage. In contrast, Formicidae contributed only 10–21% of all arthropods from the mainland site.

In general, large arthropods are well represented in sweep sample collections from mainland rainforests. On the Costa Rica site, 526 arthropods 5 mm or greater in length were collected per 1000 sweeps and this comprised 15.1% of all arthropods. Comparable figures are

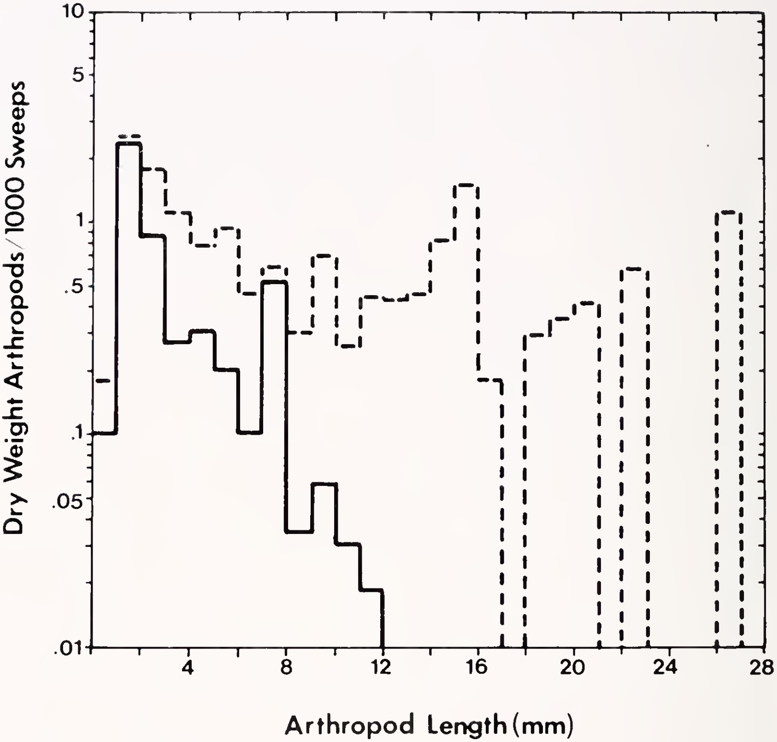

Fig. 4. Dry-weight – frequency distributions for arthropods collected in understory foliage in cacao plantations. Conventions as in the preceding figure.

available for two other lowland rainforests in Costa Rica. In wet and dry season collections, I (Andrews, 1971b) found 510–525 arthropods 5 mm or greater in length per 1000 sweeps and these comprised 22.4–31.6% of all arthropods. In a dry season collection, Janzen and Schoener (1968) found 201 arthropods 5 mm or greater in length per 1000 sweeps and this comprised 25.2% of all arthropods. In comparison, very few large arthropods were collected on Dominica, the one island locality for which comparable data are available. I collected only 44 individuals 5 mm or more in length per 1000 sweeps and only 0.6% of all arthropods collected were in this size category (Table 2).

More extensive comparisons of island and mainland arthropod communities have been made in second growth habitats. Allen et al. (1973) and Janzen (1973a, b) sweep sampled comparable sites on Puerto Rico and nearby smaller islands and on the mainland in Costa Rica. Both studies found a significantly lower abundance of arthropods in the island than in the mainland collections.

Population Densities

Anoles were two to three times more abundant on the island than on the mainland study site (Table 3). The total population size of *A. oculatus* was estimated at 299–363 individuals and of *A. limifrons*, 123 individuals. I assume that gains and losses to the adult populations during the census intervals were small because of their fidelity to established territories (Rand, 1967; Ruibal and Philibosian, 1974a; Andrews and Rand, unpub. mainland data) and because mortality would be slight during the census periods. The Peterson estimate for *A. ocilatus* juveniles is probably reasonable because the census period spanned only two weeks. However, the regression technique used for *A. limifrons* adults gave unrealistically high values for *A. limifrons* juveniles. This was the result of the large

Table 3. Population composition, density, and biomass of *A. oculatus* on the Dominica study site and *A. limifrons* on the Costa Rica study site. Estimates for each class are followed by 95% confidence limits. Asterisked values for juveniles indicate the total number captured during the census period. Two totals for *A. oculatus* are given, one for each estimate of juvenile numbers.

	A. oculatus	*A. limifrons*
Site area (m^2)	625	652
Number of Individuals		
Juveniles	170 (138–241)	—
	106*	46*
Subadult males	44 (22–∞)	—
Adult females	111 (80–198)	—
Adult males	38 (28–65)	—
Total adults	—	77 (72–82)
Total numbers	299–363	123
Total biomass (g)	1056–1121	96

number of unmarked individuals that were captured during the seven week census period. The census period was long enough to allow recruitment from eggs. Moreover, because of a lower site fidelity of juveniles than adults (Rand, 1967), appreciable numbers of unmarked individuals may have moved into the study area and marked individuals moved away from it. A conservative estimate of juvenile population size is the total number of juveniles captured on each site during the census period (Table 3). Only 22 *A. humilis* were encountered on the mark-recapture area; the inclusion of its numbers would increase the number of anoles on the mainland site very little.

For similar habitats, the commonest species on islands characteristically have higher population densities than the commonest mainland species (Table 4). In non-forested and disturbed habitats, some island species become extremely abundant. For example, densities of 1400 and 2000 individuals per 1000 m^2 are recorded for the grass anoles, *A. poncensis* and *A. pulchellus*, on Puerto Rico. Population densities of more than 400 individuals per 1000 m^2 are typical of trunk-ground anoles in disturbed habitats (e.g. *A. oculatus, A. lineatopus, A. acutus, A. sagrei*). The island species listed with relatively low densities share habitats with species of equal or greater abundance. On Bimini, although *A. distichus, A. carolinensis,* and *A. angusticeps* are generally uncommon compared to *A. sagrei,* the range of combined densities on five sites where all four species were present was 197–935 individuals per 1000 m^2 (Schoener and Schoener, unpub. data). *Anolis lineatopus* and *A. opalinus* had a combined density of 312 individuals per 1000 m^2 on Jamaica.

In contrast to the island examples, the highest densities recorded for anoles in disturbed mainland habitats are all less than 200 individuals per 1000 m^2. On Barro Colorado Island in Panama, *A. auratus,* a mainland counterpart of the West Indian grass anoles, had an estimated population density of 137 individuals per 1000 m^2 (Andrews, unpub. data) even when population densities were unusually high (A. S. Rand, pers. comm.).

Anole densities are lower in forests than in more open and disturbed habitats on both islands and on the mainland. On Abaco, Schoener and Schoener (unpub. data) estimate population densities for *A. sagrei* of 167–235 individuals/1000 m^2 on forest sites and 439–969 individuals/1000 m^2 on secondary sites over a two year period. Fleming (pers. comm.) found only six *A. limifrons* per 1000

m^2 in forest plots in the Atlantic lowlands of Costa Rica, in contrast to my estimate of 189 individuals/1000 m^2 in cacao plantations. Greater densities of some anoles in disturbed habitats compared with forested habitats has also been noted in Mexico by Henderson and Fitch (1975).

Anolis density estimates on islands and on the mainland may be even more disparate than indicated in Table 4. Sparse populations are usually not chosen for ecological study because of difficulty in obtaining sufficient data to accurately estimate population size. Since *Anolis* densities are generally lower on the mainland, mainland site selection is more likely to be biased towards high density situations.

Population densities have not been determined for any South American anoles. Work by Rand and Humphrey (1968), Fitch et al. (1976) and Duellman (in press) indicate that the most conspicuous characteristic of *Anolis* communities in this region is the extremely low densities of all species. An on-going study (Miyata, 1977) is being conducted, in part, in disturbed habitats where some species are encountered fairly frequently. It is obvious that low densities have generally discouraged ecological research on anoles in South America.

Diets

The island cacao site is characterized by low arthropod abundance, arthropod size distributions skewed towards small sizes, high frequencies of ants and a high density of *Anolis* lizards relative to the mainland site. These differences in the prey community should be reflected in the diets of the island and mainland cacao anoles.

Daily food intake of the cacao anoles was assessed from the quantities of food material found in their stomachs (Fig. 5). The two mainland species consistently had greater volumes of prey in their stomachs per gram body weight than did the island species. The differences were the greatest for the adult females of *A. limifrons* and *A. humilis* which had about twice the prey volume as did the similarly sized juveniles of *A. oculatus*. The greatest similarities were for adult males of the two mainland species which had mean prey volumes comparable to those of similarly sized *A. oculatus*.

Metabolic rate, and thus energy requirements, are a function of temperature in lizards (Bennett and Dawson, 1976). Since *A. oculatus* and *A. limifrons* seem to have similar thermal regimes,

Table 4. Population densities of island and mainland *Anolis* lizards. Original values converted to number per 1000 m².

ISLANDS

Species	Habitat	Locality	No./1000 m²
A. oculatus	cacao	Dominica (Table 3)	466–573
A. lineatopus	brush heap	Jamaica (Rand 1967)	1091
A. cristatellus	park	Puerto Rico (Rand 1961)	145
A. poncensis	cactus patch	Puerto Rico (Rand 1961)	1398
A. gundlachi	forest	Puerto Rico (Turner and Gist 1970)	200–280
A. pulchellus	grassland	Puerto Rico (Gorman and Harwood 1977)	2000
A. acutus	park	St. Croix (Ruibal and Philibosian 1974a)	430
A. sagrei	various sites	Abaco (Schoener and Schoener, MS)	167–969
A. sagrei	various sites	Bimini (Schoener and Schoener, MS)	77–685
A. distichus	various sites	Bimini (Schoener and Schoener, MS)	9–109
A. carolinensis	various sites	Bimini (Schoener and Schoener, MS)	18–69
A. angusticeps	various sites	Bimini (Schoener and Schoener, MS)	35–231
A. opalinus	pasture-scrub	Mandeville, Jamaica (Jenssen 1973)	142
A. lineatopus	pasture-scrub	Mandeville, Jamaica (Jenssen 1973)	170

		MAINLAND	
A. limifrons	cacao	Costa Rica (Table 3)	189
A. nebulosus	oak woodland	Mexico (Jenssen 1970)	90
A. polylepis	forest	Costa Rica (Andrews, unpub. data)	29
A. limifrons	forest	Panama (Andrews, in prep., Sexton 1967)	39–165
A. limifrons	forest	Costa Rica (Fleming, unpub. data)	6
A. humilis	forest	Costa Rica (Fleming, unpub. data)	11
A. cupreus	forest	Costa Rica (Fleming and Hooker 1975)	11–145
A. cupreus	wooded ravine	Costa Rica (Fitch 1973a)	57–141
A. cupreus	gallery forest	Costa Rica (Fitch 1973a)	184–191
A. auratus	grassland	Panama (Andrews, unpub. data)	135
A. tropidonotus	pine woodland	Honduras (Jackson 1973)	9
A. lionotus	stream edge	Panama (Campbell 1973)	13–100
A. poecilopus	stream edge	Panama (Campbell 1973)	13–100

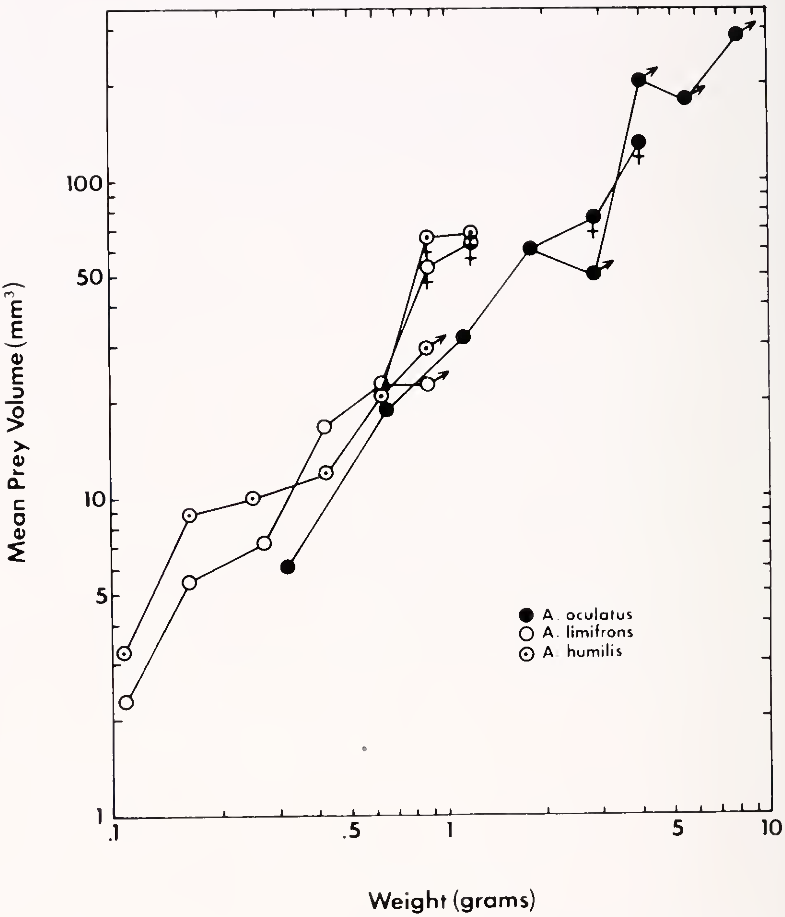

Fig. 5. Mean volumes of prey per individual for *A. oculatus*, *A. limifrons*, and *A. humilis* expressed as a function of body weight. Head lengths converted to weight equivalents with equations in Table 10.

their energy requirements should not differ on this basis. Ruibal and Philibosian (1970) measured mid-day body temperatures for *A. oculatus* in a cacao plantation near my study site. Lizards had a mean body temperature of 29.8° C for a range in air temperature of 28.6–29.8° C. A. R. Kiester and I measured mid-day body temperatures for *A. limifrons* along a path at La Lola and at the forest site in

May 1971. Body temperatures at these sites should bracket those in the cacao site because they had somewhat more open and more closed canopies respectively. Sixteen adult *A. limifrons* along the path had a mean body temperature of 30.1° C (S. E. = 0.44) with a range in air temperature of 28.0–32.0° C. In the forest, six adults had a mean body temperature of 29.3° C (S.E. = 0.21) with a range in air temperature of 28.4–30.3° C. Mid-day body temperatures of both *A. oculatus* and *A. limifrons* averaged about 30° C.

In some qualitative aspects the prey size utilization curves for the three cacao anoles are similar (Figs. 6–8). The distributions by prey numbers are all strongly skewed towards the smaller prey sizes, *i.e.* the items eaten most frequently by all species were small. Such distributions seem to be typical for anoles (Schoener, 1968; Sexton et al., 1972) and probably reflect log-normal distributions of size in insect communities (Schoener and Janzen, 1968). The distributions by prey volume are more normal in appearance although still skewed towards small prey sizes for some lizard classes. Arthropod length is related to volume (or weight) by a power function (Schoener, 1969a). Therefore, large items, although eaten relatively infrequently, contribute substantially to the volume of prey eaten and thus are more important than frequency would indicate.

Larger individuals of all species tended to take larger prey than small individuals. This was particularly clear for *A. oculatus* where differences were significant for all such comparisons ($p \leqslant .01$, Kolmogorov-Smirnov two-tailed test, Siegal 1956). Females tended to take larger prey than equally sized sub-adult males but differences were not significant (K-S two-tailed test, $p > 0.05$).

For *A. limifrons,* the classes listed in order of decreasing prey size are: adult female, juvenile II, adult males and juvenile I ($p \leqslant 0.05$ for all pairwise comparisons, K-S two-tailed tests). Thus, males took relatively small prey for their size. For *A. humilis,* males and females took prey of similar sizes but significantly larger prey than did the juvenile classes.

Although qualitatively similar, the prey size utilization curves of the island and mainland anoles differ markedly when absolute prey sizes are considered. The sampled population of *A. oculatus* took significantly smaller prey than did the *A. limifrons* population ($p \leqslant .001$, K-S two-tailed test). This difference is also illustrated from comparisons of lizard size classes (Fig. 9). The largest males were

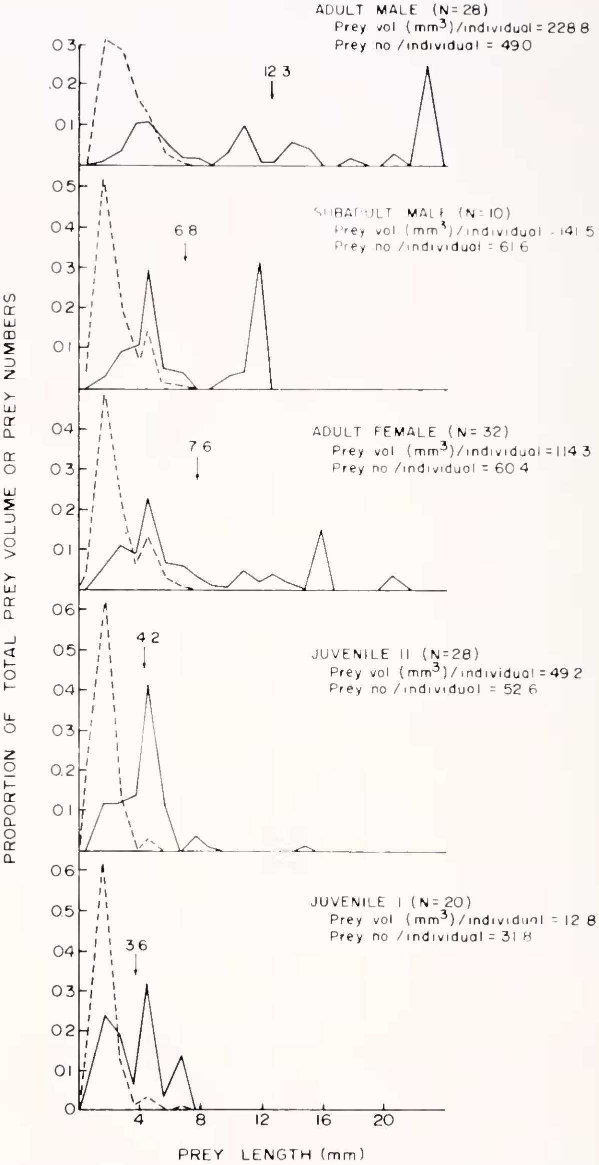

Fig. 6. Prey utilization curves by the fraction of prey numbers in each prey-length class (----) and the fraction of prey volume in each prey-length class (—) for *A. oculatus.* Arrows indicate mean prey sizes for the volume distribution.

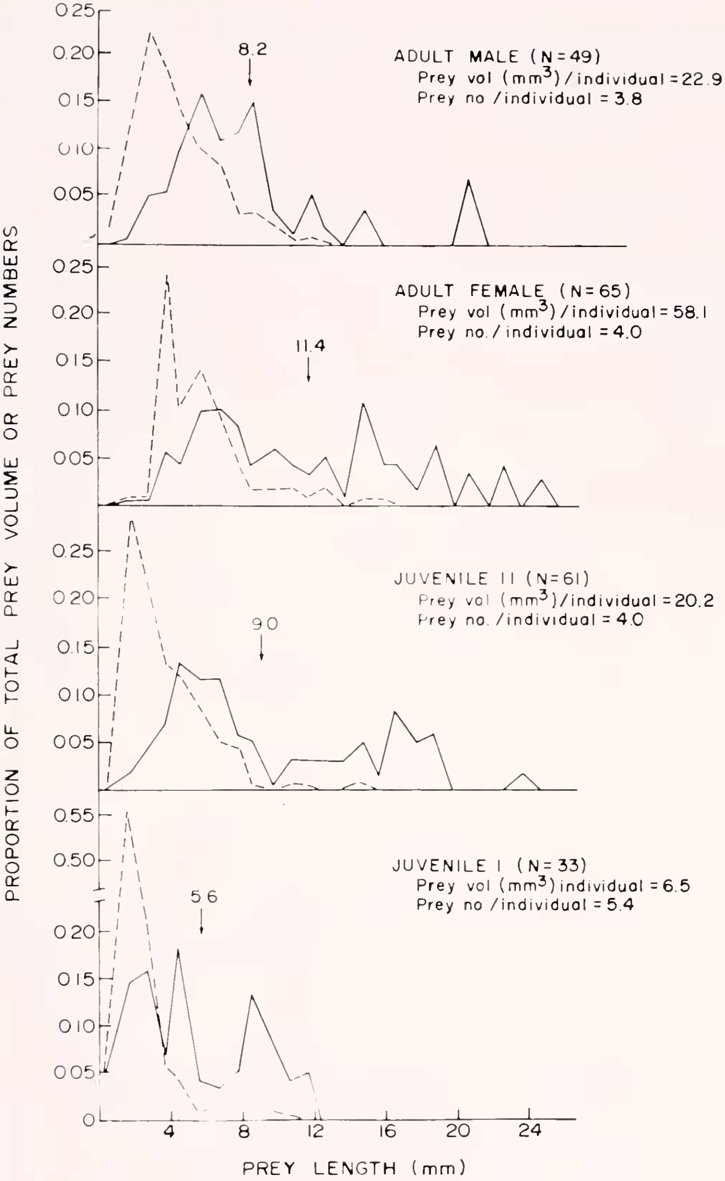

Fig. 7. Prey utilization curves for *A. limifrons.* Conventions the same as for the preceding figure.

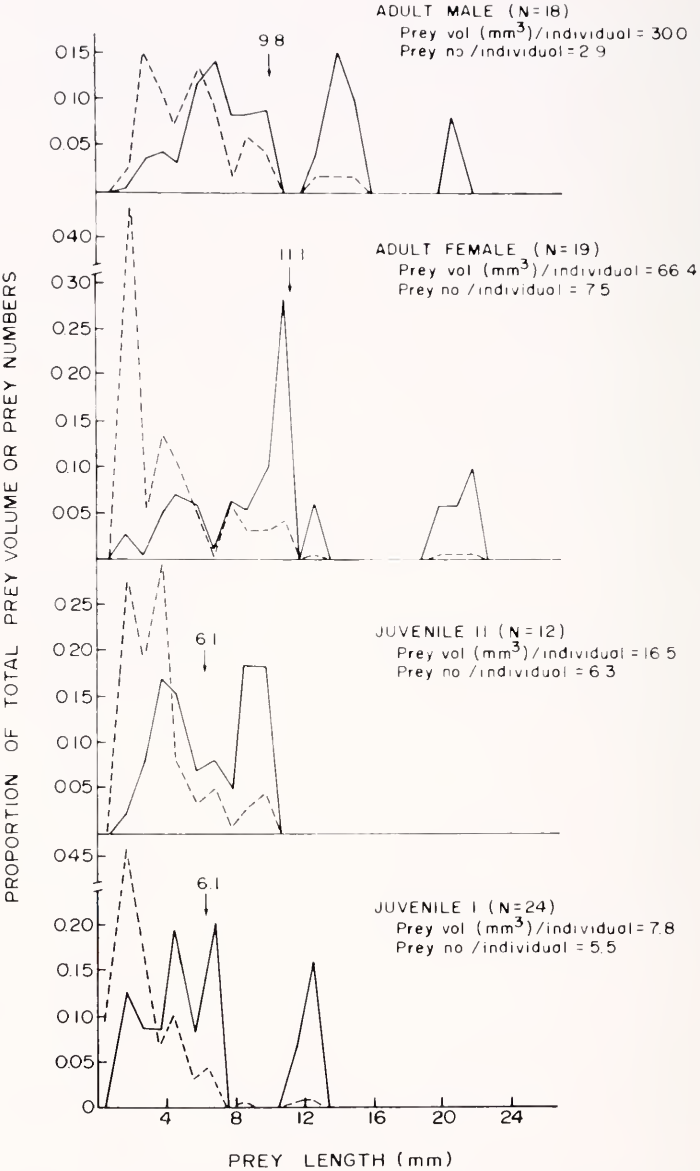

Fig. 8. Prey utilization curves for *A. humilis*. Conventions the same as Figure 6.

the only *A. oculatus* that averaged larger prey than any *A. limifrons* and this was a result of three large orthopterans eaten by one individual which strongly influenced the mean. Mean prey sizes for *A. humilis* are not plotted but are very similar to those of *A. limifrons* (compare class means in Figs. 7 and 8). However, in the comparison of the prey size distributions for the entire collection of both species, *A. limifrons* was found to take significantly larger prey than did *A. humilis* ($p \leqslant .001$, K-S two-tailed test). Associated with the differences in prey sizes were the numbers of prey found per anole individual — 32–62 for *A. oculatus* as opposed to 4–5 for *A. limifrons* and 3–8 for *A. humilis.*

The three species also differed in the taxonomic composition of their diets. For *A. oculatus,* the most frequently eaten arthropods

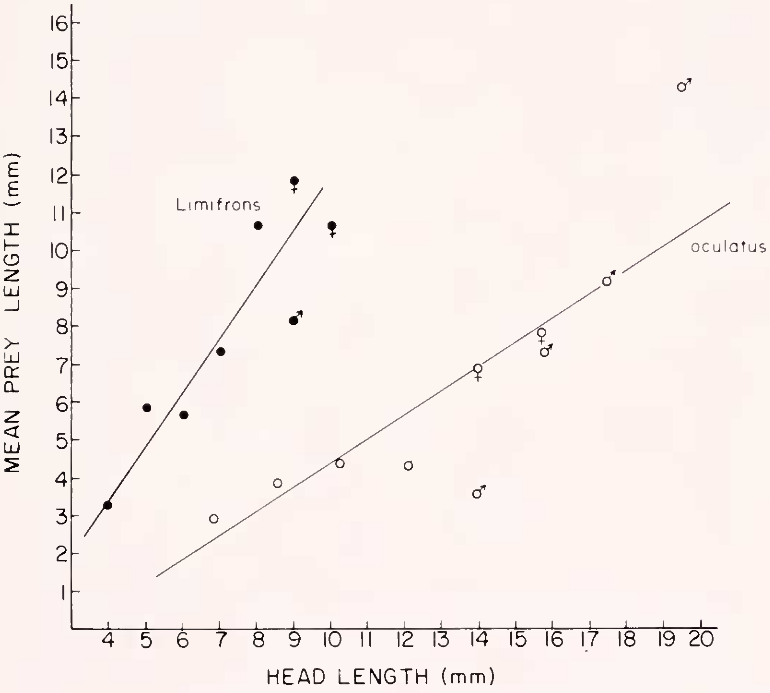

Fig. 9. Mean prey length for the volume distribution (see Fig. 6) as a function of head length for *A. oculatus* and *A. limifrons.*

were Formicidae (ants) which contributed 44–57% of all items (Table 5). Formicidae, Isoptera, and miscellaneous (mostly psocids, collembola, and mites) arthropods were the most important contributors to prey volume although decreasingly so for the larger anoles with contributions of 77, 61, 58, and 39% for juveniles, adult females, subadult males, and adult males, respectively. For *A. limifrons,* no one taxon was outstanding in frequency but Lepidoptera larvae were the most important contributor to volume for all classes (27–44%) while Homoptera, spiders, and Orthoptera were of lesser importance (Table 6). For *A. humilis,* frequency of various taxa was more consistent, with holometaboulous larvae (mostly Diptera and Coleoptera), spiders, miscellaneous, and Isopoda being consistently highly ranked (Table 7). Again the most important contributor to volume was Lepidoptera larvae (25–28%).

Stomach content analyses show that the diet of the island *A. oculatus* is made up of numerous small insects, primarily ants, and

Table 5. Dietary composition of *A. oculatus* on the Dominica site in August 1971. Values shown are the decimal fraction of total numbers and volume (mm^3) for each class.

	Juvenile		Adult Female		Subadult Male		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.001	.011	.003	.002	.002	.005	.012	.088
Lepidoptera Ad.	—	—	.001	.006	—	—	.001	.001
Orthoptera	.002	.020	.004	.035	.006	.025	.005	.300
Blattidae	.002	.023	.005	.041	.002	.006	.001	.002
Hymenoptera: Formicidae	.460	.256	.502	.244	.570	.224	.444	.206
Hymenoptera: Other	.036	.011	.008	.001	.010	.005	.009	.042
Homoptera	.006	.006	.006	.010	.005	.007	.005	.001
Hemiptera	.006	.004	.004	.004	.002	.001	.001	.001
Coleoptera Ad.	.084	.039	.067	.058	.063	.009	.191	.102
Diptera Ad.	.052	.080	.015	.144	.014	.356	.008	.067
Holometabolous L.	.012	.020	.019	.006	.013	.005	.005	.002
Araneida	.033	.019	.012	.087	.014	.005	.015	.005
Isopoda	—	—	—	—	—	—	—	—
Isoptera	.077	.377	.113	.210	.119	.274	.180	.126
Misc.	.229	.135	.242	.153	.181	.078	.124	.056
Total N	2110		1934		616		1373	
Total Volume	1633.8		3656.0		1415.2		6407.6	

Table 6. Dietary composition of *A. limifrons* on Costa Rica site in May 1971. Values shown are the decimal fraction of total numbers and volume (mm^3) for each class.

	Juvenile		Adult Female		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.153	.437	.123	.273	.179	.318
Lepidoptera Ad.	.014	.017	.054	.097	.043	.038
Orthoptera	.002	.004	.042	.125	.027	.039
Blattidae	.019	.066	.034	.120	.005	.001
Hymenoptera: Formicidae	.074	.008	.069	.008	.109	.033
Hymenoptera: Other	.108	.030	.061	.011	.038	.023
Homoptera	.108	.129	.088	.076	.147	.090
Hemiptera	.026	.005	.019	.004	.005	.003
Coleoptera Ad.	.053	.030	.161	.078	.125	.084
Diptera Ad.	.110	.056	.050	.024	.125	.049
Holometabolous L.	.026	.030	.004	.001		
Araneida	.165	.099	.119	.056	.087	.230
Isopoda	.045	.071	.142	.076	.071	.064
Isoptera	—	—	—	—	—	—
Misc.	.096	.017	.034	.051	.038	.028
Total N	418		258		184	
Total Volume	1445.4		3776.1		1122.0	

of the mainland *A. limifrons* of a few large insects, primarily Lepidopteran larvae. This dichotomy seems typical of most island and mainland anoles so far studied (Rand, 1967; Schoener, 1967, 1968; Schoener and Gorman, 1968; Andrews, 1971a, b; Sexton et al., 1972; Lister, 1976; Scott et al., 1976). If the frequency of prey by length is considered, it seems generally true that the majority of the prey of island anoles (population or class) are less than 5 mm in length and the majority of the prey of mainland anoles are 5 mm in length or more. Ants are conspicuous in the diets of island anoles only. A "giant" anole, *A. cuvieri* of Puerto Rico, seems to be an exception (Rand and Andrews, 1975), but generalizations discussed here may not apply to such a large species. This problem is discussed in the Overview Section.

Although intraspecific comparisons indicate that head and body dimensions of anoles are related to prey size (Schoener, 1968; Schoener and Gorman, 1968), comparisons between species, and

Table 7. Dietary composition of *A. humilis* on the Costa Rica site in May 1971. Values shown are the decimal fraction of total numbers and volume (mm^3) for each class.

	Juvenile		Adult Female		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.091	.281	.085	.276	.132	.254
Lepidoptera Ad.	.014	.009	.028	.090	.019	.070
Orthoptera	.039	.136	.021	.030	.076	.189
Blattidae	.005	.021	.007	.007	.019	.036
Hymenoptera: Formicidae	.082	.032	.042	.008	.094	.039
Hymenoptera: Other	.039	.012	—	—	—	—
Homoptera	.029	.036	.042	.087	.057	.037
Hemiptera	.048.	.014	—	—	—	—
Coleoptera Ad.	.048	.028	.014	.006	.132	.042
Diptera Ad.	.043	.020	.063	.135	.019	.001
Holometabolous L.	.173	.207	.507	.196	.132	.058
Araneida	.149	.039	.092	.026	.094	.089
Isopoda	.101	.142	.070	.137	.113	.127
Isoptera	—	—	—	—	—	—
Misc.	.139	.028	.028	.001	.113	.058
Total N	208		142		53	
Total Volume	386.2		1261.6		540.8	

particularly between species that occupy different habitats, show that lizard size alone is a poor indicator of prey size. For example, most sizes of *A. limifrons* eat larger prey than do *A. oculatus* even though *A. oculatus* is by far the larger species. Moreover, *A. oculatus* has a relatively longer head and greater weight per unit SVL than *A. limifrons*. There is apparently no direct functional relationship between the size and body proportions of anoles and the size of prey eaten. For *A. oculatus*, the linear relationship between lizard body size and mean prey size may result from interference competition where larger individuals monopolize the largest prey through social dominance over smaller individuals.

Anolis activity patterns

Both diets and population densities suggest that island anoles may have to spend more time and energy foraging and interacting with other individuals than do mainland anoles. If turnover rates and caloric values of stomach contents are comparable, then for similar energy requirements, the utilization of small prey will necessitate more active foraging by island than by mainland anoles. This prediction is borne out by results of observations on adult females on the cacao sites (Table 8). *A. oculatus* individuals were considerably more active than *A. limifrons* during foraging as judged by the number of shifts in position and the number of movements that were directed towards potential prey. *A. oculatus* made about twice the number of major shifts in position (greater than one body length) than did *A. limifrons*. *A. oculatus* was observed to attack prey about five times more frequently. The greater activity of *A. oculatus* was associated with a relatively shorter prey attack distance with 70% of the 60 prey capture attempts made at 10 cm or less as opposed to only 25% of the 8 such attempts for *A. limifrons*. Although *A. oculatus* females fed more on the ground than did *A. limifrons* females (85% versus 38% of attacks), the success rate of both species was similar; about 80% of prey capture attempts resulted in capture.

Where anole densities on islands are greater than on the mainland, the activities and associated energetic costs of social interactions will be greater for island than for mainland anoles. Social interactions in reptile populations appear to increase as a function of population density (Brattstrom, 1974). Presumably, increased density is associated with increased levels of interactions between males and females as well as increased levels of aggression between individuals of the same sex. Ruibal and Philibosian (1974b) found a linear increase in aggressive encounters with density for both male and female *A. acutus*. Brad Lister (pers. comm.) recorded the

Table 8. Indices of foraging activity of adult female *Anolis* on the island and mainland cacao sites.

	A. oculatus	*A. limifrons*
n	18	12
Hours of observation	9	6
Position shifts/h	12.1	5.2
Prey capture attempts/h	6.7	1.3
% successful attempts	82	75
Mean prey distance (cm)	19	30
% captures on ground	85	38

activities of adult male *A. sagrei* in areas with densities of 13 and 50 individuals per 231 m^2 on Abaco Island in the Bahamas. He found that this approximately four-fold increase in male density was associated with a 15–20 fold increase per anole in such socially relevant activities as chases and displays (headbobs and dewlaps).

High activity rates of island anoles may only be possible because of the relaxation of predation in island environments. With low risk of predation, island anoles maximize fitness by moving frequently to capture prey and to engage in social interactions with neighbors. In contrast, mainland anoles live in environments where a moving lizard has a relatively high probability of attracting the attention of a predator (Andrews, 1979). Mainland anoles maximize fitness by feeding infrequently on large, high yield items.

Observations by Toft (1976) address this point. Diurnal members of frog communities in tropical rainforests exhibit one of two foraging patterns. The poisonous dendrobatids and some bufonids are active foragers, moving almost incessantly and eating very small items such as ants. In contrast, the palatable frogs (mostly leptodactylids) are sit-and-wait predators on relatively large arthropods. Their foraging behavior is much like that of the arboreal sit-and-wait anoles. The conspicuous behavior of dendrobatids and bufonids may be possible only because they are distasteful to most predators.

Survivorship

Survivorship of adult *A. oculatus* on the island site was considerably greater than of adult *A. limifrons* on the mainland site (Table 9). Nine months after the original census of the *A. limifrons* population, none of the males that were present on the site in May were recaptured and only one (6.6% of females captured) female was recaptured. In contrast, a high proportion of the originally marked *A. oculatus* were recaptured in following censuses. After 7 and 11 months respectively, 32.6% and 25.0% of males and 62.9% and 53.5% of females were recaptured.

Although there are few long-term population studies on anoles, the evidence at hand suggests that adult survivorship is greater for island than for mainland anoles. Annual adult survivorship of *A. acutus* on St. Croix ranged from 27–40% for females and 0–19% for males (Ruibal and Philibosian, 1974a). Schoener and Schoener (1978) found annual survivorships up to 20–50% for some classes of

A. sagrei, A. distichus, and *A. angusticeps* on Bimini and Andros. Several populations of *A. opalinus* also had many adult individuals that lived for more than one year (T. A. Jenssen, pers. comm.). On the other hand, both capture-recapture data and seasonal changes in population composition suggest complete annual turnover of adults for mainland *A. polylepis* (Andrews, 1971b), *A. limifrons* in Costa Rica (Table 9; Fitch, 1973b), *A. limifrons* in Panama (Andrews and Rand, in prep.; Sexton et al., 1963), *A. nebulosus* (Jenssen, 1970), *A. cupreus* (Fitch, 1973a; Fleming and Hooker, 1975), and other mainland anoles (Fitch, 1973b).

Size Relationships

The island and mainland cacao anoles are markedly different in size (Table 10). *A. oculatus* is large and exhibits a pronounced sexual dimorphism in adult maximum size. Males reached 79 mm SVL or about 11 g and females 63 mm SVL or about 5 g. In contrast, *A. limifrons* and *A. humilis* are small with slight sexual dimorphism in size. Female *A. limifrons* reached 41 mm SVL and female *A. humilis* 40 mm SVL at weights of about 1.3 g and males were a few mm less in SVL. This difference in size and in degree of sexual dimorphism is typical of the differences between island and mainland anoles.

Sexual dimorphism ratios (SDR's) of Greater Antillean and mainland species are contrasted in Figure 10. Species size is indexed by maximum SVL of males and females (Williams, 1972). In this comparison, the number of sympatric species (as many as 6–7) are similar in both the island and mainland faunas. This comparison is

Table 9. Survivorship of adult anoles on cacao sites. For *A. oculatus* this included all individuals ⩾ 48 mm SVL.

	A. oculatus	*A. limifrons*
No. adults initially marked	44 ♂	23 ♂
	85 ♀	32 ♀
Time elapsed	7 months	3 months
Total captured (% marked)	46 ♂ (32.6)	18 ♂ (55.6)
	62 ♀ (62.9)	17 ♀ (47.1)
Time elapsed	11 months	9 months
Total captured (% marked)	44 ♂ (25.0)	18 ♂ (0.0)
	71 ♀ (53.5)	15 ♀ (6.6)

Table 10. Body size relationships of the *Anolis* populations in this study. Head length (HL) and weight (W) are given as a function of snout-vent length (SVL) with HL and SVL in mm and W in grams. Regression equations determined by least squares analysis (r^2 follows equations in parentheses).

Species	Maximum SVL		♀ SVL at Sex. Mat.	Regression Equations	
	♂	♀			
A. oculatus	79	63	48	$HL = .260 + .272\ SVL$ (.99)	$W = .000024\ SVL^{2.98}$ (.98)
A. limifrons	39	41	35	$HL = .966 + .234\ SVL$ (.97)	$W = .000048\ SVL^{2.73}$ (.92)
A. humilis	37	40	35	$HL = 1.151 + .241\ SVL$ (.99)	

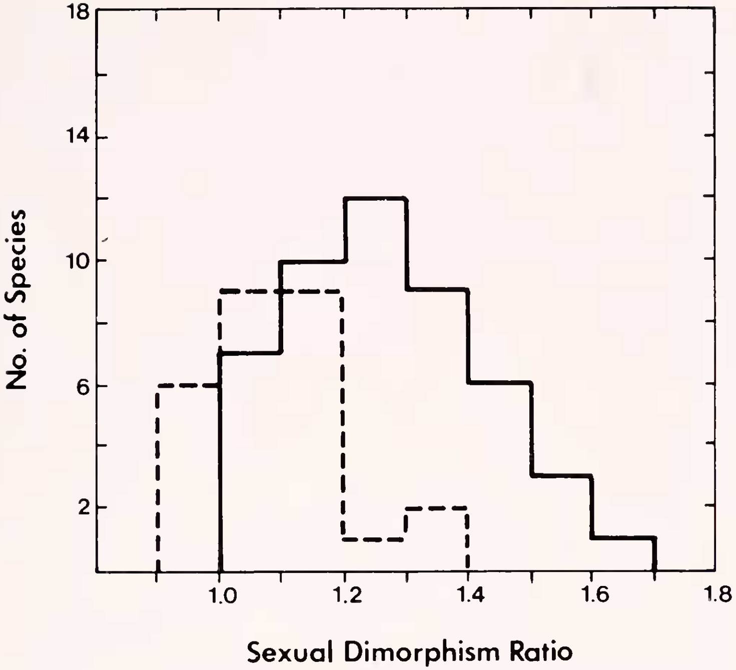

Fig. 10. Sexual dimorphism (male maximum SVL/female maximum SVL) ratios for Greater Antillean (solid line) and mainland (South and Central America) (dashed line) *Anolis*. Data for the Greater Antillean species are from Schoener (unpublished measurement tables, only species with a sample size of 15 or more individuals were used). Data for mainland species are given in Table 12.

also a conservative test of the prediction that island anoles will have higher SDR's than mainland anoles (Table 1) because of lower SDR's in the Greater Antilles than on the one- and two-species islands of the Lesser Antilles (Schoener, 1977).

Island species are found to have significantly greater sexual dimorphism ratios than do mainland species ($p \leqslant .001$, 2×2 Chi-squared test, Siegal 1956). Fitch (1976) has also measured SDR's of mainland *Anolis*. Excluding those species for which I present data, the range of SDR's (0.80–1.36) and mean SDR (1.07) for the tropical anoles in his data set are very similar to mine (Fig. 10) and further support the prediction of relatively high sexual dimorphism ratios for island anoles.

An even more relevant analysis is suggested by Schoener's (unpublished MS) demonstration that ecomorphs, which are species occupying similar structural habitats, are also similar in their sexual dimorphism ratios. Although 6–7 ecomorphs have been described (Rand and Williams, 1969), the present discussion is restricted to species whose structural habitat includes shrub level vegetation. Thus plotting the SDR's of bush-grass and trunk-ground anoles as a function of maximum male SVL shows that island and mainland species form exclusive groups (Fig. 11). For any given male size, the island bush-grass species have higher sexual dimorphism ratios than mainland counterparts. Furthermore, the island trunk-ground species have greater SDR's than all but one mainland trunk-ground species. Thus, even when similar ecomorphs are compared, the island anoles have greater SDR's than mainland species.

Comparisons of size are difficult since there is a wide range of size of different species as indexed by maximum male size both on islands and on the mainland. In the Greater Antilles the range in species size increases with the number of species per island, and on Cuba, the most extreme case, the range is from 38–191 mm (Williams, 1972). Although Cuba has by far the largest *Anolis*, the range of species sizes in the Greater Antilles is generally similar to that for mainland species where the range is from 38 to about 150 mm (Williams, pers. comm.). On the one- and two-species islands of the Lesser Antilles the range in species sizes is smaller, from 47–128 mm; extreme sizes are absent. Thus the range in species size is related to species richness; the greater range for Greater Antillean than for mainland anoles is possibly due to ecological opportunities that are not present on the mainland (Williams, 1972).

To avoid this problem I compare the relative abundance of various sized species within *Anolis* communities on islands and on the mainland.

Relatively large species are common and frequently dominant members of anole communities in the West Indies. On single species islands in the Lesser Antilles maximum male SVL's tend to range between 65 and 95 mm (Williams, 1972). On islands with two species, one tends to be larger and the other smaller than the average for solitary anoles (Williams, 1972). However, both members of these species pairs are frequently co-dominants in the habitats where they occur together (G. Gorman, pers. comm.). There are many

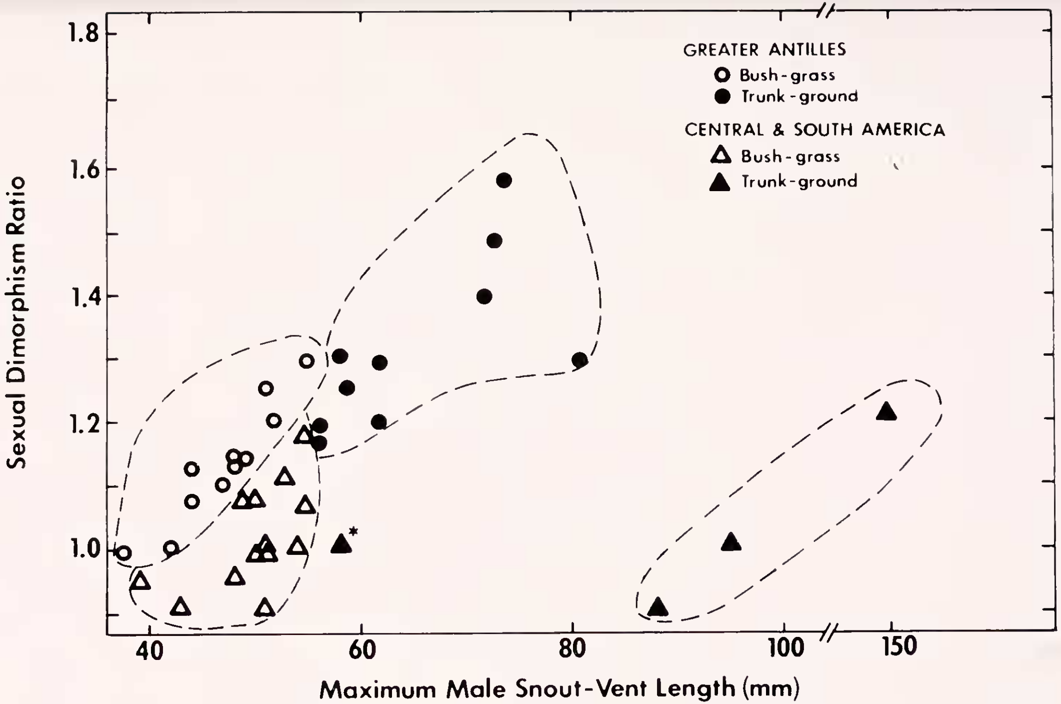

Fig. 11. Sexual dimorphism ratios expressed as a function of male maximum SVL for bush-grass and trunk-ground ecomorphs. Both sexual dimorphism ratios were plotted for the four mainland species which had two sample populations. Data sources as in Fig. 10. *A. lemurinus* is noted by an *. Although this species is a trunk-ground anole, it commonly perches in dark recesses at the base of trees (Fitch, pers. comm., Andrews, unpub. data). It is much less conspicuous than most trunk-ground anoles which typically perch in relatively high and exposed locations.

species in the Greater Antilles with maximum male sizes of 55 mm SVL or less (Schoener, unpub. measurement tables). Despite this, small bush-grass anoles and large trunk-ground anoles that are sympatric may have comparable densities (Schoener and Schoener, 1971a, b; Jenssen, 1973) or large trunk-ground anoles may have greater densities than sympatric bush-grass anoles (Turner and Gist, 1970; Rand, 1967).

In contrast to the island situation, *Anolis* communities on the mainland are either dominated by small species or are comprised entirely of species with low population densities. According to Fitch et al. (1976): "Throughout Mexico and Central America one or another of the seven species mentioned [*A. humilis, A. limifrons, A. cupreus, A. sericeus, A. nebulosus, A. subocularis,* and *A. tropidonotus*] tend to dominate habitats suitable for anoles". To his list I would add *A. polylepis,* the dominant in southwestern Costa Rica. All of these species are small, with males not exceeding 55 mm in maximum SVL. Furthermore, all species occupy shrub-level structural habitats. Large congeners are rarely encountered relative to the small dominants. Examples of large species with low population densities are *A. frenatus* in Panama (Andrews and Rand, unpublished data), *A. capito* in Costa Rica (Andrews, 1971b), *A. attenuatus* and *A. woodi* in Costa Rica (Fitch et al., 1976), and *A. biporcatus* and *A. pentaprion* in Costa Rica and Panama (Andrews, unpublished data; Fitch, unpublished data).

In South America, the species most frequently encountered may be relatively large in size. It appears that the structure of *Anolis* communities in South America may be quite different than in Central America and Mexico, but because all species are infrequently encountered, much more information is necessary before such a generalization is possible.

Because of the high abundance of large species on islands, comparisons of population density (Table 4) provide a minimal contrast between *Anolis* community structure on islands and on the mainland. For example, the total live weight of *A. oculatus* on the island study was estimated at 1094 g (including 173 juveniles) and the total live weight of *A. limifrons* on the mainland site at 96 g (Table 3). The 2–3 fold difference in numbers becomes a ten-fold difference in biomass.

Reproduction (females)

For lowland *Anolis* species, reproductive activity is associated with rainfall (Licht and Gorman, 1970). Judging from studies on sites with rainfall regimes similar to those of this study, reproduction probably continues year round for *A. oculatus* and *A. limifrons.* Possibly some dimunition occurs in the number of females with oviducal eggs during January-March (Licht and Gorman, 1970; Fitch, 1973c). Data on reproductive condition was collected during times of the year that both *A. oculatus* and *A. limifrons* females should have been producing eggs (August 1971 and April-May 1971, respectively). The majority of adult females on the cacao study sites were reproductive as measured by the presence of oviducal eggs (Table 11). A greater proportion of female *A. limifrons* were considered reproductive by this criterion than female *A. oculatus* ($p \leqslant .01$, 2 × 2 Chi-squared test, Siegal, 1956). Using reproductive condition as an index of the rate of egg production (Licht and Gorman, 1970), the data of Table 11 suggest that the rate of egg production by *A. limifrons* females might be greater than for the *A. oculatus* females.

A general comparison of reproductive effort or proportion of energy budgets allocated to reproduction (Hirshfield and Tinkle,

Table 11. Reproductive condition of female *Anolis* in study populations expressed as the number of individuals with oviducal eggs.

	Repro. class (no. of eggs)	Number of Females	% females with eggs
A. oculatus	0	13	
Aug. 1971	1	22	63
Dominica	2	0	
A. limifrons	0	6	
May 1971	1	53	91
Costa Rica	2	6	
A. humilis	0	4	
May 1971	1	13	80
Costa Rica	2	2	

1975) for island and mainland anoles is not now possible. Such comparisons require information on the rate at which eggs are produced during the breeding season as well as their caloric worth. Rates of egg production under field conditions are known for only two tropical species. *A. aeneus* on Grenada laid eggs at intervals of about 12 days (Stamps, 1975) and *A. limifrons* (both Panamanian and Costa Rican populations) at intervals of 7–8 days (Andrews and Rand, 1974). Although reproductive condition through the annual cycle has been determined for many anoles (Licht and Gorman, 1970; Sexton et al., 1971; Andrews, 1971b; Gorman and Licht, 1974; Sexton and Brown, 1977), such data cannot be used to index the rate at which eggs are laid unless environmental conditions are comparable. One confounding factor is that anoles retain eggs under dry conditions (Stamps, 1976). Thus, two oviducal eggs may indicate retention rather than high rates of production. A second influence is the year to year variation among species in fat accumulation during dry periods and its utilization for egg production during the breeding season (Licht and Gorman, 1970; Fleming and Hooker, 1975). Fat storage would facilitate high rates of egg production over short periods. Both of the above factors make the interpretation of reproductive condition data difficult. Associated energy costs of reproduction, such as territorial defence or preparing egg laying sites, are even more poorly known than the direct costs of eggs *per se*.

OVERVIEW

We are now in a position to evaluate the evolution of life histories in island and mainland *Anolis*. A critical portion of the information that has been reviewed concerns present-day conditions in these two environments. The expectation that island and mainland anoles will differ in life histories is based on supposed differences in the way that their populations are regulated. Therefore, I first consider the evidence that island anoles are food limited relative to mainland anoles.

Determinations of arthropod and *Anolis* abundance suggest that food availability is less on islands than on the mainland. My Dominica site had a ten-fold greater live weight of anoles but about one-third the dry weight of arthropods than the Costa Rican site had. Although I measured standing crop, measurements of site productivity for arthropods would presumably enhance the difference between sites. Assuming the rate of population turnover is roughly a function of individual size, production of small arthropods would be roughly comparable on both sites due to the similar representation of arthropods ≤ 8 mm in length (Figs. 3 and 4). Production of large arthropods would be greater on the mainland site because such individuals were almost absent in the island collection. Limited arthropod data from other islands support my findings (Janzen, 1973b). More conclusively, the evidence for high anole densities on islands is well documented (Table 4) and would be strengthened by use of biomass rather than numbers of individuals because of the relatively large size of common island anoles.

The sizes and kinds of arthropods in anole diets suggest that island anoles eat more non-preferred items than do mainland anoles. Like many generalized predators, anoles prefer large items to small ones (Andrews, 1971b, unpub. data; Schoener, 1969a); the number of large prey eaten should be some function of their availability to a feeding lizard. Small items, particularly ants, are relatively more abundant in island than mainland habitats and more abundant in the diets of island than mainland anoles as well. The large numbers of prey in the stomachs of island anoles is a necessary consequence of small average prey sizes. Thus, a comparison of diets suggest that while mainland anoles have the "option" of feeding on large, high yield prey items, island anoles do not.

The above comparisons constitute indirect evidence that anoles on islands are food limited relative to anoles on the mainland. In addition, comparisons of processes that are potentially energy limited would provide more direct evidence in support of this hypothesis. The growth of juveniles is such a process and is, in fact, considerably slower for island than mainland species. For comparable lowland habitats, island juveniles grew at one-half to one-third the rate of mainland juveniles (Andrews, 1976). The low growth rates of island anoles may reflect low food availability or a relatively high allocation of energy to foraging and social activities or both.

The data at hand suggest that island anoles are food limited relative to mainland anoles. The data on survivorship are in accord. Mainland anoles have greater population turnover than island anoles, presumably reflecting the greater predation intensity in mainland than island habitats. The hypothesized dichotomy in selective regimes for island and mainland anoles is strongly supported. The consequences of such differences are predictable, at least in theory. I now review the life histories of island and mainland *Anolis*.

First, is age at maturity later for island than mainland anoles? Island females were estimated to reach sexual maturity in 5–9 months as opposed to 2–4 months for mainland females (Andrews, 1976). Comparing species with similar female size, *A. lineatopus* (Jamaica) becomes sexually mature in 156 days and *A. polylepis* (Costa Rica) in 100 days. However, in *Anolis,* size at sexual maturity is a linear function of maximum size (Andrews and Rand, 1974). Thus, the later maturity of island than mainland anoles must be a function of their lower growth rates. Moreover the low growth rates of island anoles are facultative; with augmented food, rates of growth may be more than doubled (Andrews, 1976). This means that age of maturity in female *Anolis* on islands will vary with food availability.

Two observations support the prediction that reproductive effort is lower for island than for mainland anoles. First, less energy is available for the growth of juveniles on islands than on the mainland. Energy may likewise limit reproduction for island females. On the other hand, island females have the potential to lay eggs at rates comparable to those of mainland females (Andrews and Rand, 1974). Second, hatchling size is primarily a function of female size (Andrews and Rand, 1974). Island females do not have larger hatchlings than mainland females which may be related to constraints of the arboreal life styles of anoles. However, the slope of the linear function relating hatchling weight to female weight is considerably less than one. Therefore, proportionally, the caloric investment per offspring (ignoring associated costs) will be considerably less for large than for small species. For comparisons in which island species have larger females than mainland species, relative investment per offspring would be lower for island females even if rates of egg production in the two groups were the same.

High SDR's are characteristic of West Indian *Anolis.* The male is larger in all cases. However, if sexual dimorphism is solely a function of the need to partition food by size (Schoener, 1967, 1968; Schoener and Gorman, 1968), it should not matter which sex is the larger. On the mainland, the situation is quite different. For 21 of the 59 populations measured by Fitch (1976) and myself, females were larger than males.

One explanation for the larger size of males than females is sexual selection. Trivers (1972) points out that when females are clumped in space but dispersed in time by asynchronous breeding that one male can monopolize breeding. The more females potentially monopolized, the more intense will be male-male competition for this resource. These assertions are particularly applicable to *Anolis* because: 1) adult males are often associated with more than one female (Rand, 1967; Andrews 1971a), 2) females potentially mate just prior to the ovulation of each egg (Crews, 1973), and 3) male size is positively related to reproductive success (Trivers, 1972). Because of the potential for males to monopolize many females, sexual selection should be particularly effective in insular situations where *Anolis* densities may be high.

In addition to sexual selection, factors that promote fitness in females may also explain the larger size of males than females in the West Indies. Because size at first reproduction is linearly related to maximum size (Andrews and Rand, 1974) for the same growth rates, the smaller the species size the sooner females can lay eggs. If we ignore other factors, early maturity should be advantageous because age at first maturity is such an important contributor to r_{max} (Cole, 1954). Furthermore, decrease in female size lowers metabolic requirements faster than it lowers offspring size. For example, reduction of female weight from 4 g to 2 g reduces standard energy requirements by about 40% but offspring weight by only about 20%. In highly competitive situations, it may be advantageous for females to have low energy demands and yet be able to produce relatively large offspring. Thus female size may be a compromise between low energy demands and early reproduction and the ability to produce competitive offspring. This might explain Schoener's (1969b) observation that there is less variation in median female size than in median male size between islands differing in number of congeners.

The prediction that mainland anoles will be smaller in size than island anoles is supported by community level comparisons; in mainland habitats common species are generally small and in island habitats common species are both small and large. I have argued that small size is one of a suite of r-selected life history attributes adaptive in mainland *Anolis* habitats where predator pressure is high. However, large species do occur in these habitats. The large mainland anoles appear to fall into one of two ecological categories, each minimizing the risk of predation in different ways.

The very low densities of many large species such as *A. capito* and *A. frenatus* are associated with dietary specialization on large prey items. The mean length of 62 prey items eaten by 23 adult *A. capito* was 16 mm when calculated by prey numbers or 30 mm when calculated by prey volume (Andrews, 1971b). Adult *A. frenatus* eat similarly sized prey (Scott et al., 1976; Andrews, unpub. data). Individuals of 15 mm in length or more constitute less than 0.4% of arthropods taken by sweep sampling at lowland rainforest sites in Central America (Andrews, 1971b; Janzen and Schoener, 1968, Guapiles site). Therefore large anoles that specialize on rare resources must themselves be rare. Although small arthropods are much more abundant than large ones, large anoles are probably large prey specialists because the low foraging rates are adaptive in their rainforest habitats (Andrews, 1979). The tendency of the large trunk-ground species such as *A. capito, A. frenatus,* and *A. woodi* to "freeze" rather than to flee when disturbed (Fitch, pers. comm.; Andrews, 1971b) also suggests that they avoid detection by predators by long periods of immobility and highly cryptic coloration.

The mainland anoles that are both large and relatively abundant seem to be adapted to specialized habitats where predator pressure may be relatively low. The "aquatic" anoles have maximum male sizes ranging from 70–100 mm SVL (Table 12, Fitch 1976). Campbell (1973) found densities of *A. poecilopus* and *A. lionotus* up to 100 individuals per 1000 m^2 in Panama. Escape from avian predators may be relatively easy in the boulder strewn, stream side habitats where these anoles live. The "rock" anoles, with maximum male SVLs of about 80 mm, are locally abundant in Mexico (Fitch and Henderson, 1976). Here also, predator pressure may be low.

In contrast, the overriding determinant of *Anolis* life histories on islands is competition for food. Large size is one of the K-selected attributes which maximize fitness in situations where resources are limited. The contention by Case (1978) that the increased size of territorial lizards on islands is a function of a greater availability of food resources is not supported by the *Anolis* data. Both insect standing crops and the growth rates of juveniles in comparable island and mainland habitats indicate that the ratio of resource supply to resource demand by anole populations is relatively low on islands. Although food availability may provide one constraint to the maximization of body size in island habitats, it does not explain the relative increase in size of island anoles.

The dichotomy in the life histories exhibited by island and mainland anoles generally conforms to the initial predictions (Table 1). However, life history theory implies that life history attributes are invariant expressions of the genome. It is obvious from examination of *Anolis* life history attributes that while some attributes are relatively constant in expression, others are extremely plastic. In *Anolis,* attributes such as maximum size, sexual dimorphism ratios, and offspring size have easily definable values for a given population. These indicate selection for fitness under environmental conditions that are "constant" across many generations. On the other hand, growth rate, age at sexual maturity, and rate of egg production are highly variable under experimental conditions and presumably in the field as well. There has been a recent recognition that such variability may be highly adaptive in heterogeneous or fluctuating environments (Hickman, 1975; Hirshfield and Tinkle, 1975; Nichols et al., 1976). The ability of the food limited island anoles to exploit temporally or spatially abundant food by increasing rates of growth or egg production is not surprising considering the importance of early maturity and reproductive effort to individual fitness.

The life history model proposed here must be qualified in one important respect. It was developed by focusing on the major selective forces acting on island and mainland *Anolis* that live in lowland tropical environments. Although the available data support the predicted island-mainland dichotomy, only two anole ecomorphs, the bush-grass and the trunk-ground species, have contributed to these data. The anoles we know the least about, very large species, canopy species, and species that live in extreme environments, are also the most likely to prove exceptions to the model (Andrews, 1976). The trophic position of the very large anole species may very well differ from small species since many are frugivorous (Brach, 1976; Schoener, unpub. data) and some include

Table 12. Sizes and sexual dimorphism ratios of South and Central American *Anolis*.

Species	Maximum SVL		SDR	Source	Structural habitat
	♂	♀			
A. auratus	51	51	1.00	Sexton et al. 1971 (Panama)	grass
A. barkeri	101	78	1.29	Meyer 1968 (Mexico)	aquatic-stream edge
A. biporcatus	87	97	.90	Rand (pers. comm., Panama)	canopy
A. capito	88	97	.91	Andrews (unpubl. data, Costa Rica)	trunk-ground
A. carpenteri	41	44	.93	Echelle et al. 1971 (Costa Rica)	—
A. chrysolepis[1]	69	67	1.03	Vanzolini and Williams 1970 (S. Am.)	ground
	70	80	.88		
A. cupreus[1]	55	47	1.17	Fitch et al. 1972 (Costa Rica)	bush-ground
	50	46	1.08		
A. frenatus	150	120	1.25	Scott et al. 1976 (Panama)	trunk-ground
A. fuscoauratus	43	47	.91	W. E. Duellman (pers. comm., Ecuador)	bush-ground
A. humilis	38	40	.95	Table 2 (Costa Rica)	ground
A. intermedius	54	54	1.00	H. S. Fitch (unpub. data, Costa Rica)	bush-ground
A. lemurinus[2]	58	60	.97	H. S. Fitch (unpub. data, Costa Rica)	trunk-ground
A. lemurinus	79	79	1.00	H. S. Fitch (unpub. data, Mexico)	
A. limifrons	50	50	1.00	Sexton et al. 1971 (Panama)	bush-ground
	39	41	.95	Table 2 (Costa Rica)	bush-ground
A. lionotus	76	70	1.09	Campbell 1973 (Panama)	aquatic-stream edge

A. nebulosus	49	46	1.07	Jenssen 1970 (Mexico)	bush-ground
A. onca	87	67	1.30	A. S. Rand (pers. comm., Venezuela)	bush-ground
A. ortoni	48	50	.96	W. E. Duellman (pers. comm., Ecuador)	bush
A. poecilopus	71	66	1.08	Campbell 1973 (Panama)	aquatic-stream edge
A. polylepis	53	48	1.10	Andrews 1971a (Costa Rica)	bush-ground
A. punctatus	82	77	1.06	W. E. Duellman (pers. comm., Ecuador)	twig-branch
A. sericeus	50	48	1.04	H. S. Fitch (unpub. data, Mexico)	trunk (?)
A. tropidogaster	51	51	1.00	Sexton et al. 1971 (Panama)	bush-ground
A. tropidolepis	59	58	1.02	Fitch 1972 (Costa Rica)	
A. tropidonotus	55	52	1.06	Jackson 1973 (Honduras)	bush-ground
A. trachyderma	51	56	.91	W. E. Duellman (pers. comm., Ecuador)	bush-ground
A. vociferans	56	57	.98	Myers 1971 (Costa Rica)	

[1] SDR determinations available for many populations; only those for extreme SDR's are given.

[2] The two *lemurinus* are considered distinct species because of the size differences and confused state of the taxonomy of Central American anoles.

other anoles in their diets (Rand and Andrews, 1975; O. J. Sexton, pers. comm.). Furthermore, the environment may place physiological constraints on anoles in some habitats that override the biotic factors considered here. As examples, *A. onca,* which occupies xeric coastal regions of Venezuela, has a very high SDR for a mainland anole (Table 12), and the low growth rates of *A. tropidolepis* in Costa Rica may be a function of low environmental temperatures in its cloud forest habitat (Fitch, 1972). Whether or not a distinct island-mainland dichotomy can be extended to such "atypical" species is yet to be resolved.

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